

REVIEW

The Effect of Stress and Disturbance on Echinoderms

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1. INTRODUCTION

Grime [1, 2] proposed that two types of external factors limit biomass. One, *stress*, was defined as any factor that limited production; the second, *disturbance*, as any factor that partially or totally caused destruction of biomass. Habitat productivity and habitat duration, and growth rate and mortality (parameters of fitness) have been used in a similar manner [3, 4]. Stress and disturbance can be either biotic or abiotic. Grime's definition of stress is consistent with Levitt's [5] analogy of biological to physical stress: a stress produces a strain. In biological systems, the strain would be a decrease in production [6]. Levitt [5] pointed out that stresses in biological systems differ from physical ones in that the stress must be measured not in units of force, but in units of energy. Similarly, since production is best expressed in units of energy [7, 8], biological stress would result in a decrease in deposition of energy in the organism (a decrease in production). It is in this context that low levels of resources, including food for animals, may be stresses as they limit production.

Grime [1, 2] identified three primary strategies in plants, corresponding to three of the four possible permutations of high and low stress and disturbance (Figs. 1, 2). Distinct types of life-history strategies would be associated with these three strategies. *Competitive plants* (C-strategy) are adapted to low stress and low disturbance in habitats of high productivity and long duration; *stress-tolerant plants* (S-strategy), to high stress and

low disturbance in habitats of low productivity and long duration; *ruderal plants* (R-strategy, from Latin meaning "rubble" and thus, growing in a disturbed habitat), to low stress and high disturbance in habitats of high productivity and short duration. High stress would prevent recovery in highly disturbed habitats, and this strategy would not be possible.

The three primary strategies are the results of extreme levels of stress and disturbance, and Grime proposed that intermediate conditions would result in secondary strategies. *Competitive ruderals* (CR strategy) are adapted to low stress, with competition being restricted by moderate disturbance; *stress-tolerant ruderals* (SR strategy), to lightly disturbed, unproductive habitats; *stress-tolerant competitors* (CS strategy), to relatively undisturbed conditions and moderate intensities of stress; and *CSR species*, to habitats with moderate intensities of both stress and disturbance that restrict competition, or which have temporal or spatial variation in intensities of competition, stress, and disturbance.

A suite of characteristics would be associated with each strategy (Table 1). According to Grime [2, 3, 9-11], these characteristics involve the way in which energy and matter are allocated for somatic and gonadal production, maintenance, and protection from disturbance.

Competitors have access to large amounts of resources over considerable periods of time, and a high potential for resource capture. In terrestrial animals, competitors are active foragers over large areas. In aquatic animals, competitors may also be less active foragers or even stationary if productiv-

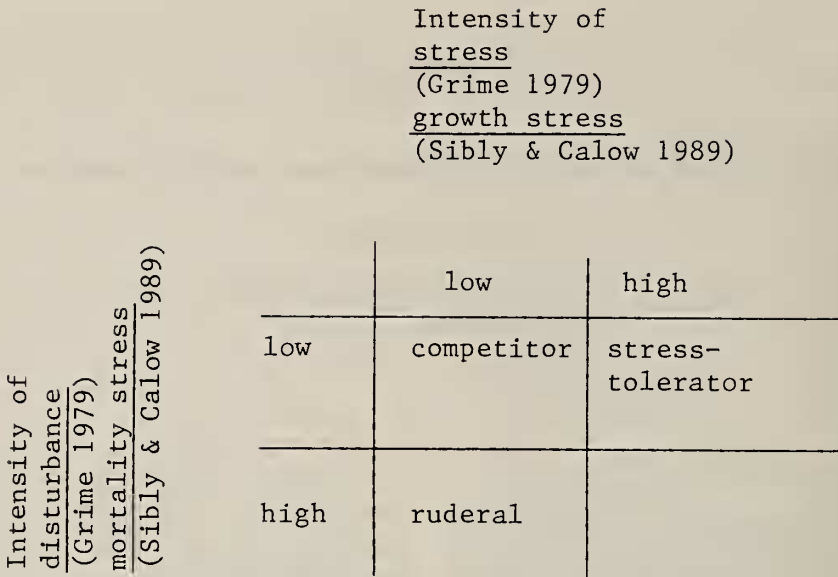


FIG. 1. Strategies resulting from combinations of different levels of stress and disturbance.

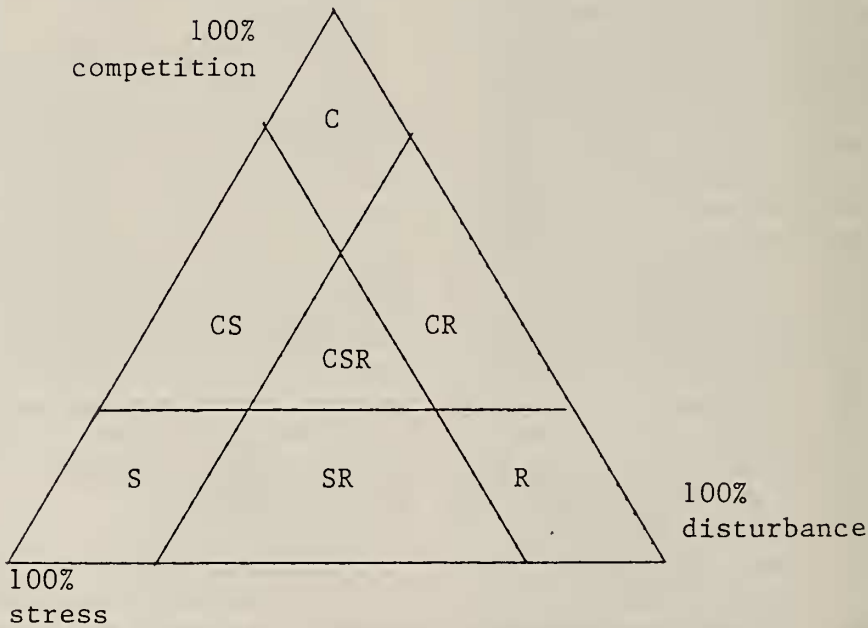


FIG. 2. Triangular model indicating the strategies resulting from combinations of different levels of stress and disturbance. C: competitor, S: stress-tolerator, R: ruderal, CS: stress-tolerant competitor, CR: ruderal competitor, SR: stress-tolerant ruderal, CRS: CRS strategist. (modified from Grime 1977)

ity is high and food is brought to them by currents. Competitors are fast growing, long-lived, and iteroparous. They reinvest captured resources in continued somatic production and activity. Be-

cause of these characteristics, Grime [3] also referred to this as a “capitalistic” strategy. *Stress-tolerators* have access to small amounts of resources (either because of the small amounts

TABLE 1. Characteristics of competitive, stress-tolerant, and ruderal echinoderms

	Competitive	Stree-tolerant	Ruderal
<i>Characteristic</i>			
<i>Habitat</i>			
Potential productivity	high	low	high
Duration	long	long	short
Stability	high	high	low
Disturbance	low	low	high
<i>Life history</i>			
Longevity	long or relatively short	long or very long	short, or very short
Phenology of reproduction	annual, pronounced cycle	many types, may be intermittent, continuous, or asexual	early in life, annual
Reproductive effort	low	low	high
Reproductive output	high	low	low or high, depending on body size
Developmental type*	2.1 (2.2?)	1, 2	1,2
<i>Physiology</i>			
Maximal relative potential for resource capture	high	low	high
Maximal relative potential growth rate	rapid	slow	rapid
<i>Miscellaneous</i>			
Defense against predation (structural, chemical, behavioral)	relatively specialized, often ineffective	if present, constitutive	relatively specialized, often ineffective
Palatability	high	if predation occurs, low	high

* Developmental types [107]: 1, Direct; 2, Indirect; 2.1, planktotrophic and pelagic; 2.2; lecithotrophic and pelagic, 2.3, lecithotrophic and benthic; 2.4, lecithotrophic and brooded; 2.5, lecithotrophic and viviparous.

available or of their mode of resource capture). In animals, stress-tolerators are passive in feeding or have limited active foraging over limited areas. Resources are captured at a low rate over a long period or time, or in brief, infrequent, unpredictable pulses. They are slow growing, and long or very long-lived. Although iteroparous, their reproduction may be irregular in time and nature; it may be suspended with chronic, severe stress.

Ruderals have access to large amounts of resources but their longevity is limited by disturbance (food exhaustion, predation, abiotic factors). They have rapid growth and early reproduction at an early age. As they are short lived, they are

semelparous or have limited iteroparity. They tend to sustain reproduction even when under stress.

Grime [2, 9] suggested that heterotrophic organisms also have the three primary strategies attributed to autotrophic plants. He placed primary significance on the response of the organism to stress, and asserted that evolutionary responses to stress fall into basic types that correspond to widely-recurrent ecological strategies that would allow all organisms, regardless of taxonomic or trophic group, to be placed in a common framework of basic functional types. His proposal has not been systematically evaluated for any

major group of heterotrophs. This review applies the triangular model to the Echinodermata, a major animal phylum of great importance in the ocean world.

2. PRIMARY STRATEGIES

2.1 *Competitive echinoderms*

The only echinoderms that clearly fit the criterion of being active foragers are some asteroids. *Acanthaster planci* of the Indo-Pacific coral reefs may be an example. It is found in a region of high resource availability and long duration, has a high potential for resource acquisition, is long lived, iteroparous with a high fecundity, and has relatively ineffective protection against disturbance [12, 13]. *Pycnopodia helianthoides* and *Meyenaster gelatinosus* are probably other examples [14, 15]. These are very active species found on the highly productive west coasts of North and South America respectively where abundant prey are available.

Among the regular echinoids, the diadematids have the highest capacity for active foraging but are not always found in habitats of high production and low disturbance. The other regular echinoids are less active. Although many are found in areas of high productivity, the temporal and spatial variation in intensities of competition, stress, and disturbance suggests that they are not competitors as a primary strategy.

Whether particulate-feeding echinoderms have the potential for a sufficiently high rate of food capture to be a competitor as a primary strategy is debatable. Dense, persistent shallow-water epifaunal ophiuroid beds are found in various parts of the world ocean [16]. These occur where flow and levels of suspended organic matter are high and the incidence of predation is low and sublethal. The dendrochirotid holothuroid *Aslia lefevrei* forms dense aggregates off the west coast of Europe where moderately strong water-flow supplies seston continuously [17, 18]. It can have a longevity of ca. 10 years or more. As a result of their susceptibility to predation, few crinoids are found in shallow-water habitats of high productivity and low disturbance. *Antedon rosaceus* may be

an exception.

It is unlikely that deposit-feeding echinoderms (spatangoids, and aspidochirotid and molpadid holothuroids) are competitors. The ingestion of inorganic sediment should reduce their potential for a high rate of resource capture.

2.2 *Stress-tolerating echinoderms*

Although their feeding mode may limit the potential for resource capture in many echinoderms, those with stress-tolerance as a primary strategy are found where food availability is very low. This occurs in the deep sea which receives only 1 to 3% of the surface primary productivity [19]. Many echinoderm species occur in the deep sea, and no class is always dominant [20]. All should be stress-tolerant strategists as a result of the low availability of food. This is correlated with their passive or low level of activity in feeding.

Perhaps the best known representatives are the stalked crinoids, now restricted to deeper waters [21]. Crinoids are passive, rheophilic suspension-feeders restricted to low-energy water habitats [22] and have little potential for capturing even the limited resources in the deep sea. Meyer and Macurda [23] suggested that the appearance of predatory teleosts led to the restriction of stalked crinoids to the deep sea. It would seem that the combination of high stress (low capacity for production) and disturbance (predation), Grime's fourth non-permissible permutation, would be responsible. Nothing is known of their life histories, but one would predict that they would be slow-growing and long-lived.

Growth of deep-sea holothuroids, echinoids and ophiuroids is slow and the echinoids there are long lived [24–32] as expected. *Echinus affinis* are thought to live up to ca. 28 years. Several holothuroid, ophiuroid, and asteroid species have low fecundity [30, 33–36], but not necessarily less than that characteristic for their taxon, size, and reproductive mode. The deep-sea pelagic holothuroid *Scotoanassa* has occurrence patterns that have been interpreted to result from reproductive responses to short-term environmental changes (probably in food availability) [37].

The tropical shallow-water asteroids are microphagous. They may be stressed by the low levels of

resources available. Blake [38] concluded that the primarily tropical valvatids and echiniasterids have extensive development of structural protection that is related to the high predation pressure in the region, and suggested that the microphagous mode of feeding was the consequence of this. To the contrary, the protection against predation may be the consequence of the stress of the low rate of resource capture and the advantage of allocating resources to increase longevity.

The echinoids *Colobocentrotus atratus* and *Heterocentrotus mammillatus* (Echinometridae) are found in extremely high-energy water in the tropics and have a low detrital food supply that constitutes an additional stress to that of physical exposure. These species have an extremely heavy test and spines that constitute a greater proportion of the body weight [39] and energy [40] than in most regular echinoids. They also have a long life-span [39, 41]. Ebert [39] noted that the survivorship of regular echinoids increases with an increase in the relative size of the body wall. He related this to the degree of exposure to high-energy habitats. The long life-span was associated with a slow rate of growth. Ebert suggested that these observations supported the hypothesis that survival is related to allocation of resources to maintenance. Rather than attributing the long life-span and slow growth to the rigors of the physical environment, one might attribute them to low resource availability or acquisition.

The suspension-feeding ophiuroid *Amphiura filiformis* would seem best classified as a stress-tolerant species based on estimated life-spans of 20 to 25 years [42, 43]. Yet a number of reports indicates life spans of only ca. 5 years [see 43]. Indeed, Buchanan [44] concluded that the species was fast growing and short-lived, dying soon after reproduction. He contrasted it to *Amphiura chiajei*, which he found to be slow growing and long-lived. This difference in characteristics reported for *A. filiformis* has been attributed to underrepresentation of juveniles in sampling [42]. It would seem that the maximal longevity found best indicates the strategy for the species. The high incidence of sublethal predation of *A. filiformis* in Galway Bay that should require a major allocation of resources [45] is not that expected to be associ-

ated with such a long-lived species. In this regard, it may be that the other suspension-feeding ophiuroids that form dense, persistent beds but suffer little predation [16, 46, 47] are also stress-tolerators. They would be comparable to the stalked crinoids that apparently cannot exist in shallow-water because of predation [23] as it combines high stress and disturbance.

Deposit-feeding echinoids (Atelostomacea and Gnathostomacea), ophiuroids (Ophiocomidae, Amphiuridae, Ophiactida, Ophiothrichidae), holothuroids (Aspidochirotida, Elaspodida, Apodida, Molpadida), and asteroids (some Paxillosida) ingest sediment that should reduce nutrient levels and should be stress-tolerators. The ophiuroid *Amphiura chiajei* shows no evidence of lethal predation, has a slow rate of growth, and is long-lived and iteroparous [43]. The spatangoid *Echinocardium cordatum* has a relatively long life-span estimated to be ca. 15 years [48]. As it lives in deep burrows [49], it should be relatively free from predation, but mortality in shallow waters as a result of storms occurs [50].

It is possible that the Antarctic echinoderms are stress-tolerant strategists. Pearse *et al.* [51] characterized the Antarctic shallow-water environment as being extremely oligotrophic most of the year, with the shallow benthos being seasonally very productive and unstable and the deeper benthos being very stable. They characterized the benthic invertebrates as having very slow gonadal development and somatic growth, and attributed this to lack of adaptation to the low temperatures. These characteristics may instead be responses to low food availability or quality. Either would result in a decrease in productivity.

Stressed echinoderms may have unusual reproductive characteristics such as little seasonality (asynchrony within and/or among individuals), intermittent reproduction, asexual reproduction, and direct development over a long life-span. The asteroid *Asterina miniata*, which feeds most commonly on detrital plant material that may limit its production [52], seems to have no predators [53] and has asynchronous reproduction [54]. The asteroid *Ctenodiscus crispatus*, which feeds non-selectively on deposits, shows asynchronous gametogenesis and aseasonal, continuous reproduction

[55]. Shick *et al.* [55] noted that the reproductive pattern in the eurybathic *C. crispatus* is similar to that of deep-sea echinoderms and suggested that it may be related to the constancy of the population's detrital food source. Similarly, Tyler [19, 29] and Tyler *et al.* [56] suggested that the high frequency of reproductive asynchrony in deep-sea ophiuroids and asteroids results from the constant level of food that provides no seasonal cues for reproduction. To the contrary, the low level of food, and not its constancy, may be responsible.

Asexual reproduction by fission occurs in a few species of asteroids, ophiuroids, and holothuroids [57]. Asexual reproduction in these species seems to be associated with low availability of food [57, 58] and thus would be a stress response.

2.3 Ruderal echinoderms

Several shallow-water, tropical regular echinoids of the family Toxopneustidae (*Lytechinus*, *Tripneustes*) seem to be ruderals. They are found in habitats of high primary production, have a rapid growth rate, high reproductive output and fecundity, and short life-spans that are associated with both biotic and abiotic disturbance [59–62].

Among the ophiuroids, several species along the French coast of the English Channel have life spans of ca. 5 years or less [63–66]. These species are found in current-washed habitats, and abiotic disturbance could be the cause of the short longevity in this productive area. The longevity of *Ophiura texturata* is less in the Mediterranean Sea than in the North Sea [66] which may result from a difference in predation levels.

Some ophiuroids have longevities of only slightly more than 1 year. *Ophiothrix fragilis* lives ca. 15 months [64]. *Amphipholis squamata* has a longevity of ca. 1 to 2.5 years [see 47]. The shorter longevities reported for this species were in tide-pool populations and were thought to result from higher stress. The simultaneous hermaphroditism and brooding habit of this species may be related to the small size of individuals and rigors of the habitat. Somatic and gonadal growth occur simultaneously in *A. squamata*, which is not a characteristic one would predict for a ruderal species as most resources should be put into reproduction, but whether the reproductive effort is actually

small is not known.

Amphipholis squamata is found in habitats with high production [67]. High production would not be associated with rubble habitats. Hendler and Littman [68] noted that the rarity of small ophiuroids in rubble remained to be explained. The rubble habitat is probably the non-permissible fourth permutation of Grime: high stress (low food availability) and high disturbance.

If the potential for high resource capture is a requisite for the ruderal strategy, it seems contradictory to conclude that some ophiuroids could be assigned to this primary strategy and not to the competitive one which also requires that potential. Differences in sizes or mode of feeding may be the explanation.

Several species of asteroids have characteristics of ruderals. *Asterina phylactica* is a small, simultaneous hermaphrodite that lives in moderate to strong currents along the coasts of the British Isles [69]. It first reproduces at 2 years, produces 1 to 3 broods, and has a longevity of up to 4 years [70]. In contrast, the closely related *Asterina gibbosa* is larger, a protandric hermaphrodite that lives in more sheltered habitats although it overlaps with *A. phylactica*. It first reproduces at 4 years, produces 4 to 7 broods, and has a longevity of 7 or more years. *A. phylactica* has a greater reproductive effort than *A. gibbosa*, a characteristic of a ruderal species. Emson and Crump [69, 70] related the life-history characteristics of *A. phylactica* to a more stressful habitat than that of *A. gibbosa* but they may be more related to a disturbed habitat.

3. SECONDARY STRATEGIES

3.1 Competitive ruderal echinoderms

Echinoderms with this strategy would have a high potential to obtain food but would be subject to moderate disturbance. This restricts the possibilities to asteroids and regular echinoids. Suspension-feeding ophiuroids and holothuroids in highly productive habitats may also have this strategy.

Leptasterias hexactis coexists with *Pisaster ochraceus* on the west coast of North America. Whereas *P. ochraceus* has characteristics of a CS

strategy, *L. hexactis* has characteristics of a CR strategy. It matures at a smaller size at ca 2 years of age and has a moderate, but shorter longevity [71, 74]. Menge [72] calculated that the energetic reproductive output of *P. ochraceus* was less than that of *L. hexactis*, but this is not indicative of the reproductive effort. He suggested that the small size and brooding habit of *L. hexactis* made it more susceptible to disturbance than *P. ochraceus* in the high water-energy intertidal habitat. As *L. hexactis* is found in a productive region and grows larger in the absence of *P. ochraceus*, it may be classified as having a CR strategy.

Another forcipulatid that seems to experience high disturbance is *Asterias*. *Asterias amurensis* has a longevity of only ca. 3 years [75], and actually becomes reproductively mature in less than 1 year under favorable conditions [76]. *Asterias vulgaris* and *Asterias forbesi* also mature at a small size in less than 1 year [77–79]. Menge suggested that massive mortality of these species results from disease and storms, and that their density consequently is less than the carrying capacity of their habitat. As with other echinoderms, growth is greatly affected by the availability of food. One population of *Asterias rubens* off the coast of Brittany grows slowly to a small size and has a longevity of more than 5 years while another grows rapidly to a large size and has a longevity of 3 years [80]. Thus *Asterias* seems to be another asteroid with a CR strategy.

3.2. Stress-tolerating ruderal echinoderms

Abiotic stress such as sublethal but non-optimal levels of temperature, salinity, exposure to air and wave-energy can affect intertidal and shallow-water echinoderms. Much stress, however, may be due to low levels of resources, either in their availability and/or in the ability of the organism to obtain it rapidly. The latter case can occur in those taxa that feed passively or have a low level of activity, and also in those whose potential for feeding is restricted by the potential for predation.

The reproductive characteristics of two species of Caribbean ophiuroids differ according to their level of exposure to abiotic disturbance and possibly to stress [81]. *Ophiocomella ophiactoides* in protected areas reproduce asexually except in a

few large individuals. Those in exposed areas have a high rate of asexual reproduction at all sizes. *Ophiatis savignyi* found in sponges reproduce asexually except for the few large individuals. Epiphytic ones are all asexual. Both of these species are small. The early reproduction at such a small size could be related to the high level of disturbance. The asexual reproduction could be an adaptation to a high level of stress (either low levels of food, the rigors of a shallow-water tropical habitat, or from the small body-size itself that limits resource capture). However, many echinoderms of similar size reproduce sexually.

Shallow-water tropical crinoids also seem to be SR-strategists. Crinoids in the tropical shallow-waters not only are stressed by the low level of resource availability and their passive mode of acquiring the resource, but suffer disturbance from predation as well. Although these crinoids have some behavioral, structural, and chemical deterrents to predation, they are not effective [82]. Predation on the crinoids is usually sublethal and the lost parts are regenerated.

Suspension-feeding ophiuroids have a similar situation of stress from low resource availability or acquisition and of disturbance from predation. Species found on coral-reef flats, Caribbean lagoons, and subtidal rocky reefs off the English coast are cryptic and show high incidences of sublethal predation [16, 46].

Representatives of several orders of echinoids are stress-tolerating ruderals. In the clypeasteroids *Mellita* and *Dendraster* the rate of feeding and growth, longevity, and relative gonadal-somatic production [83–87] are suggestive of stress-tolerant ruderals. The regular echinoid *Echinometra* is found in tropical intertidal and very shallow-water habitats, and experiences the stress of exposure and low food availability [88, 89] along with predation [61, 90, 91].

Intertidal dendrochirotid holothuroids in areas of low production can have SR characteristics. *Cucumaria curata* has delayed sexual maturity (at 3 years), moderate longevity ca. 5 years and low fecundity [92].

3.3. Stress-tolerating competitive echinoderms

These echinoderms would be subject to low

resource availability but have an active mode of resource capture. Several asteroids seem to fit this category. *Pisaster ochraceus* is mobile, if not highly active. It has delayed onset of reproduction, high fecundity, a potential high rate of growth, and a long life-span [73, 93], but is usually food limited [93, 94]. A related species *Pisaster giganteus* allocates energy to the pyloric caeca and to maintenance when stress is increased by low food availability [95].

3.4. CSR echinoderms

These echinoderms should be found where resources are relatively abundant and have an active mode of feeding, but also experience disturbance. As the potential for feeding is restricted by the presence of predators, the availability of the resources may be more apparent than real.

The asteroid *Luidia clathrata* is an active predator [96] that is subject to arm loss that affects its reproductive capacity [97]. It has a nocturnal feeding cycle, presumably predator-induced, that results in its being resource limited in the field [96, 98]. With limited food, it allocates resources to nutrient storage and reproduction rather than to arm regeneration [99]. With abundant food, it allocates resources to both arm regeneration and growth of the internal organs [100]. With limited food, not only is development of the gonads reduced, but also the capacity for egg fertilization and development [101].

The regular echinoids associated with lush algal florals of temperate waters are CSR strategists. They show temporal and spatial variation in intensities of competition, stress, and disturbance. *Strongylocentrotus* species have been studied most [see 53, 102–105]. These species have delayed onset of reproduction followed by annual reproduction for a number of years, a low gonadal: somatic production but a high potential maximal rate of feeding and production. Their protection against predation is not highly effective and their life-history characteristics are greatly affected by the level of predation. Predation by fish and sea otters on *Strongylocentrotus* species can be great on the west coast of North America. In this situation, they have low stress and low or moderate disturbance. Without this predation, stress

may become extreme as the strongylocentrotids eliminate their food resource by overgrazing. In this situation, they have high stress and low disturbance, and adopt the foraging strategy of “mobile-active search” rather than the “sit-and-wait” one used when food is abundant. An increase in the relative size of the Aristotle’s lantern in *Strongylocentrotus purpuratus* in such situations is thought to be an adaptive phenotypic response [106]. Strongylocentrotids survive low food availability with no or minimal somatic and gonadal production. Other Echinidae (*Echinus*, *Loxechinus*, *Paracentrotus*, *Parechinus*, *Psammechinus*, *Sterechinus*), and some Echinometridae (*Heliocidaris*, *Evechinus*) also seem to be CSR-strategists.

4. DISCUSSION

Grime’s model predicts that species adapted to different types of habitats will have different suites of characters. These characters sort into primary and secondary strategies involving differences in life history and physiology (Table 1). Life history characters involve reproduction and mortality. Physiological characters involve feeding, growth, and maintenance activities. Competitive and ruderal species are similar physiologically in the high potential for resource capture and growth rates, but differ in life histories as competitive species have greater longevity, a smaller reproductive effort, and a higher fecundity. Competitive and stress-tolerant species overlap in longevity (although the latter may be very long-lived) and are similar in their small reproductive effort, but stress-tolerant species have a lower potential for resource capture and growth rate, and a lower fecundity.

The criterion of longevity can be used to separate ruderal echinoderms from the competitive and stress-tolerant echinoderms. Ruderal, CR, and SR echinoderms seem to have life-spans of up to 5 years; competitive, CR, and CS echinoderms, from 5 to 15 years; and stress-tolerant and CS echinoderms, of many more years. The overlapping of longevity of the echinoderms in the different groups except for the extremes makes use of longevity as a criterion difficult.

Basic criteria separating the groups should in-

volve size at first reproduction, reproductive effort, reproductive output, and fecundity. It is important to recognize that reproductive effort is the proportion of the energy acquired by an organism that is allocated to reproduction. This is different from the reproductive output, which is simply the amount of energy allocated to reproduction, even if expressed in terms of body weight. Competitive echinoderms have a high reproductive output and fecundity. Ruderal echinoderms may have these characteristics also, but only in those that attain a large size. CS, and CR echinoderms similarly vary in their reproductive output and fecundity with individual size. Those few values for CS and CR echinoids suggest that reproductive effort is low. They continue to grow asymptotically. Fecundity is the result of both egg size and number, and is high in these groups. In contrast, fecundity is low in SR echinoderms, often involving the production of fewer, larger eggs and culminating, in those groups where the potential exists, in a few fissiparous species that produce a single new individual with asexual reproduction. The body form and location of the gonads may limit fecundity in crinoids and ophiuroids and affect their potential for the competitive or ruderal strategies.

The potential to acquire resources is the result of the quantity or quality of food and/or the ability to acquire it. The latter can result from the level of activity and/or effectiveness of the feeding mechanism. A basic criterion that immediately separates echinoderms is whether they are active or passive or relatively inactive feeders. Active feeders, defined as those that actively forage over large areas, are found only in Asteroidea and regular Echinoidea. Only they have the functional morphology that enables this behavior. The other groups range from the completely passive (suspension-feeding stalked Crinoidea and functionally pelmatozoan Dendrochirotida and Ophiuroidea) to the minimally vagile (suspension-feeding Comatulida, and some Ophiuroidea, Dendrochirotida, and deposit-feeding Atelostomacea, Gnathostomacea, Aspidochirotida, Molpadida, and Ophiuroidea). This low level of activity correlated with microphagous feeding limits the potential for resource acquisition and often involves ingestion

of low quality food.

Although this major division can be made on a broad scale, individual species within any taxon with characteristic size, functional morphology, or trophic type, will differ in their ability to acquire food. Thus, species in groups that are passive or relatively inactive in feeding can increase their feeding ability and/or be found in habitats of high production that increase their capacity to acquire resources. This is the probable basis for the appearance of some suspension- or deposit-feeding echinoderms as competitors or ruderals. For animals in general, it is necessary to take into account the particular characteristics of feeding behavior and predation in relation to production [107].

The maximal potential relative growth rate is another criterion that separates the competitive and ruderal strategies from the stress tolerant strategy. As echinoderms do not always recruit to habitats in which a maximal growth rate results, a wide range of growth rates for several species has been reported. One generally concludes that the fastest rate is the maximal potential rate. Although growth rates are usually based on linear dimensions or weights, comparisons of groups that differ in body forms, structures, and composition are difficult. If production is the criterion, growth should be measured in energy units. In no other way can the growth rate of a holothuroid be compared to that of an asteroid, or a regular echinoid to a spatangoid. Competitive, CS, CR, and ruderal echinoderms within taxa do have more rapid growth rates.

A basic characteristic of echinoderms important to understanding their strategies is their overall susceptibility to predation. Fish and crustaceans are the primary predators of echinoderms although some gastropods are also. Defense against predation can be structural, chemical, or behavioral. Structural and chemical defense uses energy that is not available for growth in size or for reproduction. Behavioral defense invariably reduces feeding and consequently production. As great longevity is important to the strategy, the presence of an effective defensive system against predation is found in stress-tolerant echinoderms. Less effective systems are found CS, CR, and ruderal echinoderms. Those stress-tolerant echinoderms

found in habitats that have less predation, such as the deep-sea, seem to lack structural defenses and should lack chemical ones as well. Similarly, those spatangoids burrowing at a depth sufficient to avoid predation do not have deterrent spines.

5. CONCLUSION

Studies on echinoderms have not considered the life-history and physiological characteristics in terms of the relative levels of stress and disturbance that echinoderms experience. Grime's model provides a context that can be used to interpret these characteristics. Most of the data available for echinoderms involve life-history characteristics such as longevity and reproductive output. Fecundity has not been documented for many species. An important characteristic that has not been studied for many species is reproductive effort. Most studies of the pertinent physiological characteristics involve the rate of growth, but even these are primarily for regular echinoids and asteroids and almost invariably are not in energetic units. Few studies except for regular echinoids and asteroids report the potential for resource capture and the quantify the availability of food. Data on both the life-history and physiological characteristics of a species are necessary before a complete understanding of their way of life is possible.

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